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TRAIL SHARING IN ANTS

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INTRODUCTION: THE KINDS OF TRAIL SHARING

A very few cases have been recorded of ant workers regularly utilizing the trails of other ant species. Forel (1898) designated as "parabiosis" the following complex behavior that includes trail sharing. Colonies of the Neotropical rain forest species *Crematogaster limata parabiotica* Forel and *Monacis debilis* (Emery) [=*Dolichoderus debilis* var. *parabiotica* Forel] commonly nest in close association, with the nest chambers kept separate but interconnected by passable openings; while the workers forage along common odor trails. Wheeler (1921) confirmed the phenomenon and showed that, in the one instance where he observed food gathering, the two species were attending membracids together. Wheeler also discovered a similar association between *Crematogaster parabiotica* and *Camponotus femoratus* (Fabricius). Both species were observed utilizing common trails and gathering honeydew from jassids and membracids on the same plants, as well as nectar from the same extrafloral nectaries of *Inga*. Not only were the *Crematogaster* and *Camponotus* workers tolerant of each other in this potentially competitive situation, they were on quite intimate terms. They "greeted" each other with calm antennation on the trails, and on three occasions Wheeler observed *Camponotus* actually regurgitating to *Crematogaster*.

It has not been established whether parabiosis is mutualistic or parasitic in nature. The distinction must be a subtle one in such a complicated relationship. The form *"parabiotica"* of *Crematogaster limata* is evidently always associated with other ants. If future taxonomic studies prove it to be a species distinct from *limata,* it is a likely parasite. It would then be shown to be dependent on its associates, while the latter species often nest and forage by themselves. But the *prima facie* case for mutualism seems even stronger. The broods are never mixed, and as Weber (1943) points out on the basis of his own studies, all of the parabiotic species participate vigorously together in nest defense. There is no evidence that the presence of the *Crematogaster* harms the other species, except possibly by competition for the same food resources. On the contrary, *Camponotus femoratus*

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maintains flourishing populations in localities where virtually every colony lives in parabiosis with *Crematogaster*.

While the Neotropical parabionts are doubtfully mutualistic, the relationship of the European *Camponotus lateralis* (Olivier) and *Crematogaster scutellaris* (Olivier) can be classified as weakly parasitic. Goetsch (1953) and Kaudewitz (1955) have described instances in which *Camponotus* workers followed the *Crematogaster* trails in large numbers to the *Crematogaster* feeding grounds and exploited the same food resources during the same time of day. The *Crematogaster* were hostile to the *Camponotus,* which assumed a crouching, conciliatory "Wartestellung" on meeting the host workers. Unlike the Neotropical parabionts, the two species nest separately. Moreover, the relationship is not obligatory on the *Camponotus lateralis,* since the colonies of that species are often found far removed from *Crematogaster* colonies.

I will now describe a third example of trail sharing which I recently discovered between the dolichoderine *Azteca chartifex* Forel and formicine *Camponotus beebei* Wheeler. This case is of additional interest in that it seems to illustrate a close approach to the third or neutral class of symbiosis, namely commensalism.

AZTECA CHARTIFEX AND CAMPONOTUS BEEBEI

During a trip to Trinidad, West Indies, in 1961, my attention was drawn to *Camponotus beebei,* a formicine ant previously known from only several specimens collected in Trinidad and British Guiana. On each of three occasions on which the species was encountered, twice at Spring Hill, Arima Valley, and once near Cumuto Village on the Aripo Savanna, workers were found running over tree trunks along the odor trails of the much more abundant and aggressive dolichoderine *Azteca chartifex.* The *Camponotus* were never found away from the *Azteca* trails. Extended observations at Spring Hill revealed that the *Camponotus* always followed the *Azteca* trails for long distances with fidelity equal to that maintained by the *Azteca* themselves. That this was true trail symbiosis was further evidenced by the fact that no other alien species remotely approximated such behavior. Workers of several other arboreal species occasionally blundered into the same *Azteca* files but ran abruptly away without tracing the main route of the files.

One of the Spring Hill *Camponotus* nests was located. It was in a dead, hard branch of a mango tree that had fallen and lodged in the crown of a three-meter-tall grapefruit tree in a citrus plantation. The *Camponotus* workers were seen to emerge from their nest holes, run

Fig. 1. Minor worker of *Camponotus beebei* Wheeler from Spring Hill, Trinidad.

down the mango branch to the branches of the grapefruit tree, which held an *Azteca* colony, and follow the *Azteca* trails to the ground. The *Azteca* workers seldom ventured up to the *Camponotus* nest. The *Camponotus* occupied scattered flat galleries in the mango branch. When cut apart the nest yielded 2 winged queens, 16 males, 6 major workers, 36 minor workers, and several larvae and pupae in various stages of development. The mango tree, from which the *Camponotus* colony fragment had evidently recently fallen, was also occupied by *Azteca chartifex*. In a second locality at Spring Hill, *Camponotus* workers were tracked up into the foliage of a tonka bean tree (*Dipteryx* sp.) beyond a large *Azteca* nest, but the *Camponotus* nest was not found. Nevertheless, it was evidently separate from the *Azteca* nest.

Both the *Azteca* and *Camponotus* followed the *Azteca* trails to the bases of the nest trees. Presumably both foraged extensively on the herbaceous ground vegetation, but their diets were not determined. Regardless of the nature of the diets, competition between the two species was reduced by the existence of opposite diel schedules. The *Camponotus* foraged apparently exclusively during the day, at the time the *Azteca* files were at their lowest ebb. In the early evening the number of *Azteca* workers on the trails were seen to increase by as much as a hundred-fold, but not a single *Camponotus* worker was found through several hours of searching during this time.

The *Camponotus* workers, then, "borrow" the *Azteca* trails when the owners put them to minimal use. The *Azteca* workers on the Spring Hill trails were hostile to the *Camponotus* workers and attacked them on the rare occasions when the latter slowed in their running, but the *Camponotus* were larger and faster and usually easily avoided their hosts without causing any visible disturbance. The *Camponotus* were never observed to interfere with the *Azteca* in any other way.

On the basis of the first observations it could still be legitimately asked whether the *Camponotus* were merely using the same visual or tactile "landmarks" on the tree trunks as the *Azteca,* rather than following their odor trails. This possibility was eliminated by the following experimental result. A freshly killed insect was pinned to the trunk of a tree one meter beneath the trail along which both species were running but within the range of occasional *Azteca* scouts. Within ten minutes, two *Azteca* workers had found the insect and laid odor trails from it back to the main trail. In the next five minutes over 100 *Azteca* workers moved back and forth along the new trail to the insect. In the same interval three *Camponotus*

workers, a major and two minors, approached along the main trail and, on reaching the junctures of the new trails, departed down them for various distances. The major went all the way to the insect and prowled around it for several minutes before returning to the main trail. In two subsequent replications of the experiment, two of thirteen and one of five *Camponotus* workers passing along the main trail were deflected onto the *Azteca* side trails during the period of peak *Azteca* response to the baits. Such deviations from the main trail were never observed except at this time. It was concluded that the *Camponotus* respond to the *Azteca* communication.

The following observation led to the further conclusion that the *Camponotus* were tracking the *Azteca* olfactorially rather than visually. Occasionally around midday the *Azteca* were unusually scarce on the main trail, while the *Camponotus* remained moderately common. Stretches of 30 to 50 cm. of the trail were often bare of *Azteca,* but many individual *Camponotus* followed the established track just as well. On close examination I found no alterations in the surface structure of the main trail, other than the postulated chemical one, that could have supplied the *Camponotus* with a clue.

Although the *Camponotus beebei* utilize Azteca trails extensively, the following observation shows that they have maintained their own, private trail system. On a single occasion in February a line of seven *Camponotus* were seen moving along the main *Azteca* trail. Four of the workers ran in a tight group directly behind the leader, frequently advancing enough to touch the abdomen of the ant ahead. When the leader was touched, it dashed forward at a faster pace over a short distance. This part of the behavior was typical of communication by "tandem running", which I have described earlier in a paper on the genera *Cardicondyla* and *Camponotus* (Wilson, 1959). The remaining two workers followed at a greater distance, tracing each twist and turn taken by the leader. During the next 15 minutes several other *Camponotus* workers passed the same way, again tracing parts of the route of the leader with close fidelity. After that time, new Camponotus workers continued to run on the *Azteca* trail but ignored the *Camponotus* trail. There could be no doubt that the lead ant had secreted an odor trail of the recruitment type (see Wilson, 1963). It was laid on top of the *Azteca* trunk trail, which for most of its length was about 10 centimeters wide. Equally interesting was the fact that only the *Camponotus* responded to it. The *Azteca* workers continued to pass along their own trail during the episode but failed to orient to the inner track followed so closely

by the *Camponotus*. Thus the *Camponotus* workers appear to respond to two odor trails, while the host *Azteca* respond only to one.

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ABSTRACT

Trail sharing is a rare event in ants. Of two previously described cases, one is interpreted as part of a relationship that is either mutualistic or weakly parasitic, probably the former, and the other as part of a weakly parasitic relationship.

A third, new case has been discovered which appears to be commensalistic. On Trinidad, West Indies, workers of the rather scarce formicine *Camponotus beebei* utilize the arboreal odor trails of the abundant dolichoderine, *Azteca chartifex*. The *Camponotus* "borrow" the latter's trails during the day, when *Azteca* foraging is at a low ebb. The *Camponotus* workers are treated hostilely by the *Azteca* workers but are too swift and agile to be caught; their presence does not disturb the *Azteca* seriously. On a single occasion *Camponotus* workers were observed to lay their own private recruitment odor trail on top of the *Azteca* trails. The *Camponotus* trail lasted for about fifteen minutes and had no visible effect on the *Azteca*.

LITERATURE CITED

FOREL, A.
1898. La Parabiose chez les Fourmis. Bull. Soc. Vaud. Sci. Nat., 34: 380-384.

GOETSCH, W.
1953. *Vergleichende Biologie der Insekt-Staaten*. Geest und Portig K.-G., Leipzig. 482 pp.

KAUDEWITZ, F.
1955. Zum Gastverhältnis zwischen *Crematogaster scutellaris* Ol. mit *Crematogaster lateralis bicolor* Ol. Biol. Zentralbl., 74: 69-87.

WEBER, N. A.
1943. Parabiosis in Neotropical "ant gardens." Ecology, 24: 400-404.

WHEELER, W. M.
1921. A new case of parabiosis and the "ant gardens" of British Guiana. Ecology, 2:89-103.

WILSON, E. O.
1959. Communication by tandem running in the ant genus *Cardiocondyla*. Psyche, 66: 29-34.
1963. The social biology of ants. Ann. Rev. Entomol, 8:345-368.